THE LARVA AND SPAT OF THE CANADIAN OYSTER

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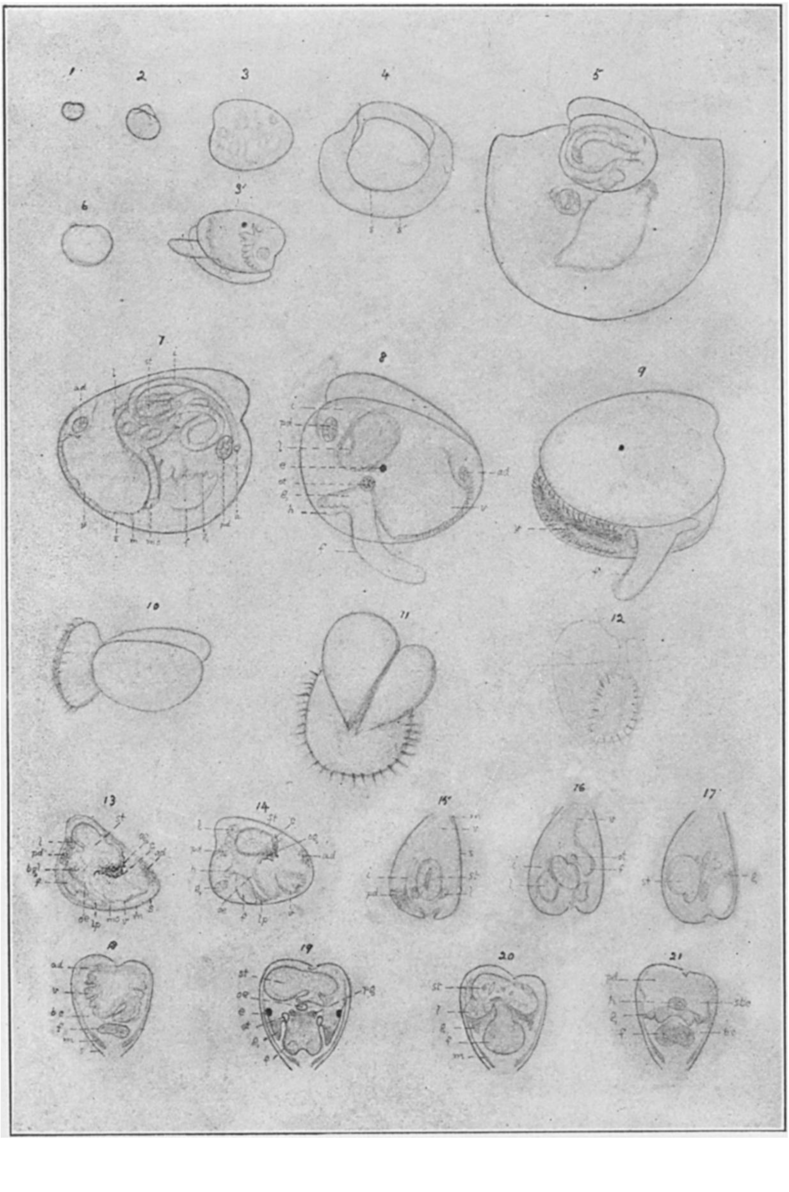
I. The Larva

In the summer of 1904, at Malpeque, Prince Edward Island, on behalf of the Canadian Marine Biological Station, I undertook to gather what information I could upon the life of the oyster from the time it becomes a distinct bivalve veliger to the time when it is recognizable by every oyster fisherman as a spat oyster.

Brooks, of Johns Hopkins University, Baltimore, to whom belongs the immortal glory of having discovered that American oysters are unisexual and that artificial fertilization of the eggs and rearing of the larvæ are possible, had worked out the spawning, fertilization, segmentation, gastrulation and organization up to the earliest microscopic free-swimming bivalve veliger, and there was no lack of literature on oyster culture beginning with macroscopic oyster spat of, let us say, the size of one's thumb-nail. But the intermediate stages, mostly microscopic, seemed to be scarcely, if at all, known, and there were many questions as to the time and place where they might be found as well as to their anatomy and comparison with other genera which required investigation.

The possibility of raising young oysters from eggs and keeping them alive without admixture with other individuals or other species until one had seen the whole series of continuous transformations into the adult seemed next to impossible. I chose rather to learn to recognize the larval oyster in plankton collections, a method which had apparently received no attention. I



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EXPLANATION OF PLATE

a, anus; *ad*, anterior adductor muscle; *bc*, branchial chamber; *bgl*, byssus gland; *c*, chitin; *e*, eye spot; *f*, foot; *g*, gills; *h*, heel of foot; *i*, intestine; *l*, liver; *lp*, lower lip; *m*, mantle; *mo*, mouth; *oe*, œsophagus; *og*, supra-œsophageal ganglion; *ot*, otocyst; *pd*, posterior adductor muscle; *pg*, pedal ganglion; *s*, larval shell (prodissoconch); *s'*, spat shell (dissoconch, nepionic); *sbc*, suprabranchial chamber; *st*, stomach; *v*, velum.

FIGS. 1, 2, 3, 4, 5. Development of Canadian oyster from bivalve veliger to young spat. From the right side, drawn under the same conditions throughout, Leitz microscope, oc. 3, obj. 2 (revolver). Zeiss Zeichenapparat. Drawing desk flush with stage and slanting upwards at proper angle to prevent distortion.

Measured under Leitz oc. 5 and obj. 4 with a Leitz oc. microm. valued by a Leitz stage microm.

FIG. 1. Oyster larva, young straight hinge stage. .089 mm. high, .103 mm. long.
" 2. Oyster larva, early umbo stage. .138 × .144 mm.
" 3. Oyster larva, full grown. .31 × .34 mm. Fig. 3′ from the left side.
" 4. Oyster spat, with the valves of the larval shell (prodissoconch) plainly retained. .51 × .55 mm.
" 5. Oyster spat. .876 × 1.030 mm. The larval shell is .369 ×.384 mm.
" 6. Same as Fig. 1 drawn under oc. 3, obj. 4, for comparison with Figs. 7, 8, 9.

FIGS. 7, 8, 9. Same as Fig. 3 drawn under oc. 3, obj. 4.

FIG. 7. Oyster larva from the left, with several organs sketched in.
" 8. Same from the right, with dorsal hinge-line tilted towards the observer.
" 9. Same from the left, with ventral gaping margin tilted towards the observer.

FIGS. 10, 11, 12. Free-hand drawings of full-grown living oyster larvæ, not so highly magnified as Figs. 7, 8, 9.

FIG. 10. Oyster larva, full-grown, from the left, velum protruded and partly expanded.
" 11. Same from behind, attached to the slide by its fully expanded velum, large left valve.
" 12. Same from the ventral surface, velum partly protruded.

FIGS. 13, 14, 15, 16, 17, 18, 19, 20, 21. Sections of full-grown larvæ, drawn free-hand.

FIG. 13. Section median sagittal (nearly), from the right. The foot being turned sideways was not split medially.
" 14. Same of another series.
" 15. Section horizontal (upper), from above.
" 16. Same (deeper).
" 17. Same (lower).
" 18. Section frontal, transverse (anterior), from behind.
" 19. Same (median).
" 20. Same (near middle) of another series.
" 21. Same (posterior) of same series as 18 and 19.

had never seen an oyster larva or a young spat, but I had followed the main stages in the life history of the mussel.

Beginning my plankton-collecting at the end of the first week in July, it soon became apparent that there were many species of bivalve larvæ present in the water, and in order to refer these with some precision to the proper adults it would be necessary to carry on at the same time a faunistic study of the Mollusca of Richmond Bay. The commonest of these relative to my purpose were found to be species of Mytilus, Mya, Venus, Clidiophora, Ostrea, Anomia, Mactra, Modiola, Pecten, Saxicava, Macoma, Ensis, Yoldia, etc., and to find larvæ corresponding to all of them was beyond my ability. Nevertheless, several larval forms gradually became familiar and I referred them provisionally to certain adults. On the twenty-fifth of July what I took for oyster larvæ (Plate, Fig. 3) first decidedly claimed my attention and as time went on I became more and more convinced of the correctness of my surmises. But belief is not proof, so I set to work experiments with a view to entrap oyster larvæ on glass plates at a time when presumably the larvæ become too heavy to swim with ease, settle towards the bottom, creep about and select some clean, solid surface upon which they fix themselves and transform into the youngest oyster spat. This was successfully accomplished on the sixteenth of August when I obtained a minute oyster spat (Fig. 5) still preserving most evident characteristics of the larva, but with the addition of a rim of spat-shell, and later I found many minute spat-oysters on various natural objects such as shells and stones.

The plankton was collected in conical nets, made of fine-meshed silk bolting cloth, attached at the broad end by a rim of linen to an iron ring one foot in diameter, to which were tied, at equal distances, three pieces of cod-line, the other ends being brought together and secured to a towing line. The small end of the net was also

furnished with a linen rim in which was tied the neck of a wide-mouthed bottle. To the towing line, in front of the net, was fastened a sinker and the whole was dragged through the sea-water, behind the little steamer *Ostrea*, under reduced speed, for about a mile, when the net was hauled up, the contained water carefully drained through one side, after which it was dipped several times right side up into the sea and raised so as to wash all the plankton material down into the bottle. The bottle could then be removed and corked, the net washed by throwing it overboard again open, and other bottles used for different places or different depths on the same excursion.

In such a manner may be procured a wealth of plankton material, but slight modifications in mode of operation may be employed, depending upon the nature and object of one's research. The older bivalve larvæ are compact, heavy, well protected, so that they will stand comparatively rough usage. By the time one reaches the laboratory the great mass of the copepods may be dead and sunk towards the bottom of the bottle, but underneath this mass one can see the darker, granular, more sand-like bivalves. These may be withdrawn by a glass tube and emptied into a watch glass, the more superficial, lighter things being again removed by a pipette. In this way bivalve larvæ may be obtained, sometimes by thousands, and almost entirely free from admixture with other animals, while among them, if collected at the proper time and place, will occur oyster larvæ.

At Malpeque the full-grown, free-swimming, pelagic, or more or less abyssal, or creeping larva of the oyster (Figs. 3, 7, 8, 9) possesses a characteristic brownish-red color—suggestive of the soil of its native island shores—a shade which enables it to be immediately distinguishable from every other bivalve larva with which it is associated. The shell (prodissoconch) is asymmetrical, inequivalve and inequipartite, the left valve being larger, more convex and with a large umbo, the right one smaller, flatter

and with a moderate umbo, while the umbos have a postero-dorsal position, projecting backwards and upwards and making the shell broader, deeper, squarer behind and tapering but rounded in front. The largest measure about .358 by .365 mm. in height and length, but, owing to the different convexities of the valves, the greater breadth above and behind, and the different degrees to which it may be tilted in this way or that, the same larva may vary much in apparent size and shape according as to how it is presented to the observer. The following are measurements of half a dozen larvæ at different ages selected from a large number of records: .131 x .138 mm., .138 x .144 mm., .207 x .241 mm., .241 x .276 mm., .296 x .345 mm., .345 x .372 mm. The larval shell of the young spat (Fig. 5) measures .369 x .384 mm. and may be taken to represent the maximum size.

When mounted on a slide the larvæ are accustomed to remain quiescent, and from their deep coloration are difficult to examine, but sometimes a more transparent one permits certain organs to be traced. When freshly collected and examined in a watch-glass of pure, cool water from their native habitat, many of them exhibit the greatest activity, swimming hither and thither or circling round and round by means of the velum (Figs. 9, 10, 11, 12), a swimming organ which they protrude between the antero-ventral margins of the shell-valves and expand in a manner resembling the opening of an umbrella. The margin of this is densely covered with large cilia, the violent flapping of which propels the animal forwards with the heavy body and shell suspended beneath the velum. Jarring the watch-glass will cause the animal to immediately withdraw its velum (Figs. 7, 8), at the same time snapping the valves of its shell together and dropping towards the bottom. Such observations illustrate the ordinary mode of locomotion and the response to violent movements in the sea, for during heavy gales a plankton net will take few or no larvæ near the surface.

An organ of immense interest to zoologists and of vast

importance to the animal is the foot (Figs. 7, 8, 9), a structure which I claim the privilege of having first recognized. The adult oyster is normally a quiescent, sessile animal, having its left valve solidly cemented to a rock or another shell. Under these conditions a creeping foot, such as is possessed by a clam, a mussel, or a quohog, would be of no service to the oyster, which in fact has none. Influenced, no doubt, by this difference in the adults, zoologists have been accustomed to think of the oyster larva as being vastly different from other bivalve larvæ, and repeatedly state that it has no foot, a misconception which justifies the view with which I started out, viz., that plankton stages of oyster larvæ have been neglected, embryologists jumping from early veliger or phylembryo to late prodissoconch or early nepionic periods. The foot, at the period we are studying, is well developed, and is a most capable organ, by means of which the animal can creep rapidly about and forcibly flop its heavy shell from one side to the other. When extended it is a long, slim, ciliated, muscular outgrowth from the middle of the ventral surface of the body of the larva, behind the velum. Its lower or posterior surface sometimes appears flattened or even grooved lengthwise (Figs. 18, 19, 21), and at a short distance from the base of attachment there is a heel-like projection (Figs. 8, 9, 13, 14, 21) which doubtless contains the opening of the byssus gland. When quiescent the foot is shortened, retracted and closely tucked away behind the velum and between the gills, but it can stretch so far as to perform feeling movements over all parts of the body within the shell and even bend up along the outside of the shell. I have no doubt that at the end of the free-swimming period, when the velum fails as an organ of locomotion and the larva has to remain at the bottom, the foot then proves to be of greatest service in freeing the little animal from overwhelming sediment, creeping on to a solid substratum, clearing a suitable place for fixation, and perhaps furnishing a transitory byssus.

Lying against the inner sides of the shell-valves are right and left folds of the mantle (Figs. 7, 18, etc.), the free edges of which secrete the shell material and may, like velum and foot, at times protrude beyond the margin.

Along each side underneath the mantle, past the base of attachment of the foot to the body, lie the gills (Figs. 7, 8, 9, 19, 20, 21), extending backwards and downwards to near the posterior edge of the shell; in the oldest free-swimming larva there are about eight filaments in each series, diminishing in size from before backwards, the last ones being mere knobs; their lower ends are free, but their upper ends spring from one continuous fold that, behind the foot, joins its mate of the opposite side, near the margins of the mantle. They correspond to the right and left inner gills of the adult oyster.

The alimentary canal (Fig. 7) is much longer than the body and in consequence has become folded, the greater part lying to the left (Figs. 17, 19, 20) of the median sagittal plane, but mouth, œsophagus and anus are median. The mouth (Figs. 7, 13) is a funnel-shaped opening lying immediately below and behind the velum, to which its walls are attached and with which it is protruded and withdrawn, so that it can only be functional while the velum is to some extent expanded, when the activity of its cilia may also contribute to the process of feeding. The œsophagus (Figs. 7, 13, 14, 19) lies between velum and foot in the median sagittal plane as well as in or very near the median transverse plane of the body. Here it passes dorsalwards, between the first gill-filamets, and opens into the stomach with its large brown lateral liver-sacs. The intestine passes backwards towards the right and then forwards towards the left, when it again turns backwards and upwards in the left umbo and finally downwards in the median plane over the posterior adductor muscle.

In front and above the velum is an anterior adductor-muscle (Figs. 7, 13, 18, etc.), running transversely between the valves, while below the posterior parts of the

umbo is a larger, transverse posterior adductor muscle (Figs. 7, 13, 21, etc.). Retractor fibers converge from the velum to points in the umbos and there are intrinsic muscle fibers in the velum, the foot and the mantle.

About the center of the animal, as viewed from one side, and anterior to the gills are two conspicuous, black pigment spots (eye specks, Figs. 3, 8, 9, 19) that, in transverse sections of the larvæ, are found to be situated right and left on the lateral walls of the body, just in front of where their ectoderm becomes continuous on to the outer surface of the first gill filament.

Immediately behind and below the pigment spots, but on a deeper level, are right and left otocysts (Figs. 8, 9, 16, 19), each containing about a dozen otoconia. Sections show them to be placed laterally in the proximal part of the foot, close to where its ectoderm passes over on to the inner surfaces of the first gill-filaments. Between the otocysts, and of course behind the œsophagus, are the two connected pedal-ganglia (Fig. 19), and at the center of the base of the velum, in front of where the œsophagus joins the stomach, is the supra-œsophageal ganglionic mass (Figs. 13, 14), protected in front by what appears to be a yellowish-brown, flexible, chitinous layer which gives origin to the muscle-fibers of the velum.

Transverse, sagittal, and horizontal sections (Figs. 13–21) of oyster larvæ, prepared in the usual way by decalcifying the shells, staining in alum-cochineal, embedding in paraffin, sectioning with a Yung microtome, and mounting on a slide in Canada balsam, have contributed much towards an accurate understanding of the relative positions of the organs.

Development naturally begins with small, simple eggs and proceeds to larger and more complex larvæ. By the time I had become oriented with regard to the latter and proved to myself that they can actually metamorphose into oyster spat it was of course too late for that season to obtain and follow the growth of the youngest larvæ. Examination of preserved plankton collections, however,

although far from being as satisfactory as fresh, living material, shows oyster larvæ (Figs. 1, 6) but little older than the stages at which the observations of Brooks closed, viz., six days old from the date of fertilization. Brooks did not give measurements, so that it is impossible to be exact on this point—I can only judge from the shape and organization. Plankton collected July 11, 1904, between Curtain Island and Ram Island contains an abundance of minute, transparent bivalve larvæ (phylembryos) in what may be known as the straight-hinge stage to distinguish them from the older larvæ with high umbos (the umbo stage) that obscure and modify the hinge line. A hasty and superficial observation of these combined with the fact of their occurrence in proximity to oyster beds might easily lead to the conclusion that they are all oyster larvæ. But they are not. Many of them are clams, a few are mussels, and one in a great number is an oyster. A full statement of how I have determined this would require too great a digression and will be dealt with in another paper, but it results from a comparative study of bivalve larvæ in the different localities of the Biological Station combined with researches into the distribution of adult forms. Adults of the above-mentioned genera are easily distinguished; the full-grown larvæ less easily, for, since they bear little resemblance to the corresponding adults, other marks of distinction have to be selected; but the young larvæ are still more difficult, for, according to the biogenetic law, the younger they are the more nearly they resemble some stage of the common original ancestor and of course approach one another in likeness. Under such conditions the practicable, distinguishable characters may again be different and require a more critical scrutiny. Since I first turned my attention to bivalve larvæ I have found it necessary to change my point of view and mode of procedure. One can not safely trust to the eye in judging proportions, but must resort to a definite and unvarying method of measuring by means of ocular and stage micrometers.

For each of the commonest species a table of lengths was prepared, jumping only one of the smallest units of my ocular micrometer at a time, and the heights were filled in as individuals of these lengths occurred. Thus larvæ of the mussel, the clam and the oyster, at the period we are considering, measure as follows:

	Length.	Height.	Length of hinge-line.
Mussel	15	10	11
Clam	15	13	10
Oyster	15	13	7

—a table which will immediately make apparent the truth of many of my statements. The eye can easily perceive a difference in the proportions of the mussel and the clam, but it requires a certain refinement of judgment to do the same for a clam and an oyster. Such an oyster larva actually measures .103 x .089 mm. in length and height, and has a short, slightly concave hinge-line of scarcely half the length of the shell.

I have said that in collections of straight-hinge larvæ but one in a great many is an oyster. A similar statement might be made for any period in the larval existence of the oyster. Upon one occasion when the umbo-stage was most abundant I estimated that there was only one oyster among twenty-five bivalve larvæ. Another time I found that when the plankton net was towed at the surface against a wind it caught about a quarter as many oysters as in going back over the same distance with the net sunk a few feet below the surface of the water.

I am of opinion that the study of plankton collections for bivalve larvæ will be found a most useful help in determining the breeding season—that is to say the height of the breeding season. From the foregoing pages it may be concluded that oyster larvæ are present in the water from the eleventh of July to the first September, and that oyster spat are present from the sixteenth of August. This would seem to indicate that the second half of August is taken up with the last stages of growth of late larvæ and that the period of growth of the masses

falls between July eleventh and August sixteenth. Taking it that the youngest larvæ I have described are little older than those of similar shape and structure described by Brooks, and allowing a possible retardation on account of the climate, we should conclude that the eggs were deposited pretty close to the first of July. That spawning does not take place much before this I judge from the fact that in 1905, while I was at Malpeque preparing the station for removal, I took plankton at intervals between June seventh and twenty-sixth and this shows no oysters and but few mussels and clams.

In the microscopic examination of the genital organs for the purpose of determining the time of sexual maturity, unless one examines a very great number taken from many different localities, he may light upon an abnormal number of individuals that are immature or that have already spawned and so form a wrong conception as to the period of maximum spawning. Combination of both methods should give the best possible results.

I have purposely attempted to disregard the statements of others in order to be entirely unbiased as to my results, and from the facts of my own observations I am disposed to think that the period of maximum spawning falls in July, but that a few may spawn earlier and a greater number may straggle in later.

It is a matter of regret to me that it did not fall to my lot to begin the study of oyster larvæ during the first summer at Malpeque, for then I could have used the second summer to verify, fill in details, and follow out suggestions. I have looked forward ever since for an opportunity to do so, and this is my chief excuse for the delay in publishing these results.

Chief points of importance resulting from the foregoing work are:

1. Larval oysters are present suspended in the water of Richmond Bay, Prince Edward Island, in July and August.

2. They may be taken in a plankton net at the surface and at various depths.

3. All stages from the freshly fertilized egg to the full-grown larva must be there.

4. The free-swimming period is, perhaps, considerable, close on a month.

5. They feed and grow, while in the free-swimming state, through a straight-hinge to an umbo-stage.

6. Normal fixation takes place when the larval shell is about .38 m. in length, and then the spat period begins.

7. A metamorphosis occurs through loss of larval organs as velum, foot, eye-spot, otocysts, etc., and a development of new organs as spat-shell, additional gills, palps, etc., is begun.

8. The larval shell is asymmetrical, as is also to some extent the contained body.

9. A foot, homologous with that of mollusks in general, is present in the older larvæ.

10. The otocysts contain otoconia.

11. Pedal ganglia are present.

12. A byssus-gland is present.

13. Gills are present.

14. Eye-spots are present.

15. A rigid system of measurements has been used, and a comparison of actual sizes at different periods of growth introduced.

16. Numerous niceties of structure, shape, color, activity, time, place, etc., are noted.

17. The spawning period has been limited.

18. Attention is directed to the importance of these theses and observations as bearing upon problems and methods of oyster culture.

Literature

European works referring to the development of the oyster larva are those of:

1. 1854. Lacaze-Duthiers. Mém. sur le dévelop. des Acéphales Lamellibr. *Comptes Rendus heb. des Séances de l'Acad. des Sciences*, Paris, XXXIX, pp. 102–106. Nouvelles observ. sur le dévelop. des huîtres. Same vol., pp. 1197–1200.

2. 1882 ('83). Horst. A Contrib. to our Knowl. of the Develop. of the

Oyster (*Ostrea edulis* L.). Bull. U. S. Fish Com., II, pp. 159–167, 12 figs.

3. 1884 ('86). Horst. The Develop. of the Oyster (*Ostrea edulis* L.). Rep. U. S. Fish Com., pp. 891–910, Pls. I and II.
4. 1883. Huxley. Oysters and the Oyster Question. *Eng. Illus. Mag.*, Oct. and Nov., pp. 47–55, 112–121.

American work must be considered to have originated with Brooks, whose discoveries inspired investigators at home and abroad and pointed the way to possibilities and methods of culture that were ably carried forward by Ryder, Winslow, Rice and others. Of the many papers, reprints, summaries, etc., published by Brooks I mention but one:

5. 1880. Brooks. Development of the American Oyster. Rep. of the Com. of Fish. of Maryland, pp. 1–18, 10 pls.
6. 1882 ('83). Ryder. On the Mode of Fixation of the Fry of the Oyster. Bull. U. S. Fish Com., II, pp. 383–387, 9 figs.
7. 1882–83 ('84). Ryder. A Sketch of the Life-history of the Oyster. 4th Ann. Rep. of the U. S. Geol. Surv., pp. 317–333, pls. 73–82.
8. 1882 ('84). Ryder. The Metamorphosis and Post-larval Stages of Development of the Oyster. Rep. U. S. Fish Com., X, pp. 779–791.
9. 1884. Ryder. A Contrib. to the Life-history of the Oyster. Fisheries and Fishery Industries of the U. S., Sec. I, pp. 711–758.
10. 1882 ('84). Winslow. Rep. of Exper. in the Artif. Prop. of Oysters. Rep. U. S. Fish Com., X, pp. 741–762.
11. 1889. Jackson. The Develop. of the Oyster with Remarks on Allied Genera. *Proc. Bos. Soc. Nat. Hist.*, XXIII, pp. 531–556, 4 pls.
12. 1890. Jackson. Phylogeny of the Pelecypoda. *Mem. Bos. Soc. Nat. Hist.*, IV, pp. 277–400.

Canada has done little towards a scientific study of oyster development. Three rather unpretentious articles are known to me.

13. 1895 ('96). Prince. Peculiarities in the Breeding of Oysters. Special Reports, Ottawa, pp. 10–13.
14. 1904. McBride. The Canadian Oyster. *The Canadian Record of Science, Montreal*, IX, July, pp. 145–156, Figs. 1–4.
15. 1905. Stafford. On the Larva and Spat of the Canadian Oyster. THE AMERICAN NATURALIST, Boston, pp. 41–44. (Preliminary to this paper.)

Brief Notes and Criticisms

Brooks (No. 5, p. 25, of the preceding list) says: "All my attempts to get later stages than these failed, etc." He refers to his Figs. 44 and 45 which were perhaps a little younger than my Fig. 1 and were six days old. I never could understand the claim that they might develop to this stage in twenty-four hours.

Horst (2, 165; 3, 904) was unable to get stages older than his Fig. 12, a straight-hinge shell of .16 mm., which according to Ryder (7, 791) would be equivalent to an American larva of half this length, *i. e.*, little younger than my Fig. 1. He adds: "I have also been disappointed in my attempts

to procure oysters in these phases of development by means of catching larvæ floating about in the sea.''

Ryder's papers (6, 383; 7, 328–9; 9, 727) are not easy to correlate on account of discrepancies in measurements or magnifications, age and occurrence, a misuse of the term embryo, etc. Making allowance for these, and combining his statements in the probable order in which they were written, I conclude that Ryder had seen two stages approximately of the same age as two I have figured. His Fig. 1, magnified 183 times measures 14.5 mm., which would give the larva an actual length of .08 mm. His Fig. 3, magnified 96 times, measures 29 mm. and similarly gives the young spat an actual length of .3 mm. But his were both fixed, and in fact it was this property which in Ryder's methods afforded the chance of their being observed. He appears to have believed that the larger one (C. 1/80 in.) marked the proper stage of fixation but that under ''favorable circumstances'' larvæ of the size of the smaller might become fixed and then grow to the size, shape and structure of the larger, at which time they first become spat. Considering that he obtained the small ones but once, that they were attached in no regular position, and that the one figured was on its right side instead of on its left, it seems more probable that the fixation was of a transitory nature (as regarded by Jackson) or that it was abnormal, due to unfavorable artificial conditions and that the normal process is for the larva to remain free until it reaches the size of the prodissoconch in the umbo of the young spat shell. Ryder's view of the duration of the free-swimming period as limited to twenty-four hours comes nearer to a possibility if we remember that he doubtless had in mind this case of abnormally early fixation. A similar statement might be made with regard to the sentence ''The difference in magnitude between the oldest artificially incubated fry seen by me and that of the youngest fixed embryos which I collected is very small.'' These also agree very well with the larvæ raised by Brooks and by Horst. He never saw larvæ between these two stages in size. This represents a period during which the larvæ had to grow to nearly four times their former diameter and undergo a very great increase of organization. If the smaller stage can be raised as in Brooks's larvæ in six days the larger might require four times six days additional, making a month for the complete larval development. This time according to Brooks, Ryder and others might be reduced by very warm weather. It is just possible that too high a temperature of small isolated quantities of water may be one of the adverse conditions which have prevented larvæ from being raised beyond this stage. In nature they not only have a broader source of food supply but they can also sink into cooler water.

Winslow (10, 757) thought that the oyster larva is predisposed to fix itself very soon after segmentation and when the shell is developed to a slight extent the larvæ remain quiet in one place at the bottom. I can believe that they do not by their own efforts travel very far from the place of their origin for their locomotion is largely a circling or to-and-fro movement, but while suspended in the water they may be transported by tidal currents.

Jackson (12, 300) wrote: ''Between the stage Fig. 25 and our next stage, Pl. XXIV, Figs. 1, 2, there is a blank in the knowledge of the

development of the oyster. It has not been described in the European species, and all attempts to obtain it in our own species have failed. In artificial confinement the oyster dies at this stage.'' His Fig. 25 is Huxley's cut of a straight-hinge larva. Figs. 1, 2 of Pl. XXIV are Jackson's own youngest stage of the spat, obtained August 4, 1888, on glass put in a drain-pipe trap on a sand-bar in Buzzard's Bay. It was firmly attached by the ventral margin of the left valve and as it had been attached less than twenty-four hours the anatomy and shell must have been developed while it was a free larva. The figures measured 37 mm. and as they are magnified 120 diameters the actual length of the recently free larva, now a fixed spat, was nearly .31 mm.

Prince (13, 13) makes the statement: ''I captured many small embryo-oysters several miles from any known oyster areas,'' but as no measurements or drawings accompany the paper one can not judge of their size or age.

McBride (14, 151, 153) says: ''Judging from the size of free-swimming larvæ caught by the tow-net . . . . During the latter part of the month (August) the waters were swarming with larvæ which, from their exact agreement in shape and appearance with the larvæ of the European oyster, were doubtless the later stages of the free-swimming young of the Malpeque oyster. . . . The later larvæ which were captured by the tow-net are characterized by possessing a straight hinge to the shell. . . . Fig. 4. Late Larva of the Oyster captured by the Surface-net.'' The so-called late larvæ are in the light of my researches in reality somewhat early larvæ. Late larvæ would be more appropriately applied to the umbo-stage which doubtless was in the water at the time referred to, but was at that time unknown as a plankton organism. The statement that the waters during the latter part of August were swarming with young straight-hinge oyster-larvæ does not correspond with what I found at the same place the succeeding year. Upon examining Fig. 4 I find that it is not an oyster larva. The measurements are 83, 70, 51 mm. which if divided through by 5.53 will give 15, 12.6, 9.2 mm. as the length, height and hinge-line. Referring this to the table of comparison of a mussel, a clam and an oyster at this period, on a former page, it becomes evident that it could have been no other than the larva of the clam.

The shell of the larva was held to be perfectly symmetrical by Ryder (6, 384; 7, 329; 8, 787; 9, 727), but Jackson (11, 541; 12, 312) observed in his youngest spat that the lower left valve was larger and deeper than the upper right one.

A foot has been mentioned by Lacaze-Duthiers, Horst, Brooks and Jackson. Lacaze-Duthiers (1, 105) said: ''En avant de l'anus un appendice pen saillant simule un rudiment de pied.'' Horst (2, 162) stated that ''A foot-like prominence is developed, whereby the animal assumes some likeness to a young gastropod.'' Brooks (5, 53) wrote: ''Near the center of the ventral surface—the top of Fig. 32—there is a well-marked and constant protuberance of the body wall, which occupies the region which, in most molluscan embryos, gives rise to the foot, and which may perhaps be regarded as a rudiment of that organ.'' In the same paragraph and referring to the same figure he mentions ''the primitive digestive cavity'' and on page 68 ''the primitive digestive tract opens by a wide blastopore.''

No one would claim that the part referred to in these extracts is the same organ as I have described in very much later larvæ. Referring to Horst's 1882 Fig. 6 or 1884 Fig. 10 we observe that it is only an accidental prominence, since it is bounded below by the invagination of the blastopore and above by that of the shell-gland, and further it disappears later on as in 1882 Fig. 10 or 1884 Fig. 14. Jackson (12, 302) affirmed: ''The nearest approach to a foot known in the developing oyster is that shown in Fig. 24, p. 299 (after Horst), and I discovered no traces of a foot in my youngest specimens.'' The best that can be said about all references to a foot at these early stages is that, by comparison with other species, they indicate the place where, at a later date, through growth and specialization, a foot as well as several other parts are formed between the mouth and the anus.

''Otocysts . . . here recorded so far as I am aware, for the first time,'' was written by McBride (14, 153), but a similar statement occurs in Lacaze-Duthiers of 1854 p. 1200, ''Enfin j'ai vu apparaitre les-otolithes . . . quelques globules agités de mouvements . . . dont personne n'avait même constati l'existence.'' McBride's ''Fig. 3. Larva of Oyster, six days old'' shows two otocysts, and in the near, right, one is a single otolith. There is something wrong about this. The oyster has about a dozen otoconia in each otocyst, a fact which Lacaze-Duthiers was perhaps aware of when he wrote the words ''quelques globules.'' If McBride's Fig. 3 properly represents his observations then it is not an oyster but a clam which I know to possess a single otolith in each otocyst. Clams are very abundant along the beach immediately below where the station stood at Malpeque and it is a reasonable inference that this larva was taken up in the water used. On the same page occur the words ''shell-gland . . . mistaken by Brooks for the gut.'' This was first pointed out by Horst in 1882.

Regarding the presence of a byssus Ryder (6, 383; 7, 329; 9, 758) was doubtful. Horst (3, 907) believed that he had noticed a small byssus. Jackson (12, 303) concludes that the oyster does not have a byssus at any period.

The absence of gills as well as the mention of symmetry in the following extract is only one of the indications that Ryder's (8, 787) conception of an oyster larva was constantly associated with the straight-hinge stage of the phylembryo: ''One of the most conspicuous differences between the symmetrical larva and the young spat is the absence of gills in the former and their presence in the latter . . . two gill pouches . . . outer gill pouches.''

Jackson (12, 303) studied the gills of the youngest spat stage and knew them to be the right and left innermost gills of the adult. He also mentions palps but says little about them. Jackson's study of the gills was so thorough and in general his observations were so exhaustive, considering the limited material, that it is worth while being cautious before suspecting him of an oversight, but I can not help thinking that what he took for palps was nothing but the foot. His figures (12, Figs. 1, 2) show it immediately behind the already shrunken velum and overlapped by the anterior gill-filaments. The two transverse lines may have been due to its being crumpled up, and the split towards the end of the ventral surface may have suggested two palps.

MONTREAL, Oct. 8, 1908.